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AEC Research and Development Report

EFFECT OF THERMAL SHOCK ON
VULNERABILITY TO PREDATION IN
JUVENILE SALMONIDS

I. SINGLE SHOCK TEMPERATURE

NOVEMBER 1972

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IN JUVENILE SALMONIDS. I. SINGLE SHOCK TEMPERATURE*

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November 1972

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ABSTRACT

Thermally shocked juvenile rainbow trout and Chinook salmon were selectively preyed upon by larger fishes under controlled laboratory conditions when both shocked and control fish were offered simultaneously. Relative vulnerability to predation increased with duration of sublethal exposure to lethal temperatures. Significant increases in predation rates were found at thermal doses above 10% (Chinook) and 20% (rainbow) of the doses causing complete body inversion. The effects were partly reversible. Quantitative measures of harmful effects from sublethal thermal shock allows their use in designing safe thermal releases into aquatic environments.

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INTRODUCTION

Many juvenile salmonids in the central Columbia River pass seaward involuntarily with river currents. Acute thermal shock can occur to those fish swept through the mixing zones of heated discharges such as those downstream of thermal power plants. Exposures to lethal high temperatures may occur in situations where temperatures are extremely high or where rates of fish passage are slow through zones where discharges and river water mix. More often, however, exposures are of sublethal duration even though the temperature encountered may be within the lethal range established by laboratory thermal resistance testing (e.g., Brett, 1952). Sublethal exposures appear to predominate in thermal effluents discharged from the plutonium-production nuclear reactors at the U.S. Atomic Energy Commission (AEC) Hanford Works on the Columbia River above Richland, Washington. Although the effects of high temperature exposure in thermal plumes may not be directly lethal, other factors acting subsequent to thermal shock may induce mortality.

One factor affecting survival of migrating salmonids under natural conditions is predation by larger fishes (Ricker, 1941; Thompson, 1959; Roos, 1960). Predatory fishes and gulls have been observed in the vicinity of the Hanford reactors during the annual spring seaward migration, suggesting the possibility of active predation. The objective of this study was to determine whether sublethal exposures of juvenile salmonids to a single, potentially lethal shock temperature (such as may occur at Hanford) can measurably increase the rate of predation. A subsequent paper will describe the effects of a range of shock temperatures for a species.

To assess this effect, a method of testing relative performance of prey fish in the laboratory was adopted from Bams (1967), who compared the performance of hatchery-reared and wild sockeye salmon. Measures of absolute performance, and of changes in this performance with variations of an environmental factor such as temperature, must be obtained from accurate measurement and/or rigid control of all factors affecting the predation situation. These complex and interacting factors include predator recognition, energy supply and delivery systems of the prey, predator and prey densities, predator hunger, rate of searching by the predators, and several others. The possible components of functional responses in predation have been described by Holling (1966). Unless tests separated in time are rigidly controlled and performed under near identical conditions, comparison of absolute performance data is difficult. Differences among individual test animals provide additional obstacles to precise comparison of results.

For groups of fish simultaneously available, a simplified procedure was developed by Bams (1967) that accurately measures relative performance. It not only identified differences between groups in ability to evade predators, if such differences exist, but it quantifies those differences in relative and comparable terms. The procedure involves simultaneous testing of two groups of fish under identical conditions in one tank with the same predators. It does not require accurate control or measurement of the actual conditions, as long as they are favorable for proper functioning of the predator and prey organisms.

MATERIALS AND METHODS

Juvenile Chinook salmon, Oncorhynchus tshawytscha (Walbaum), and rainbow trout, Salmo gairdneri (Richardson), were used as prey fish. These species are abundant in the Hanford area of the central Columbia annually from April to August (Park, 1969; Mains and Smith, 1964).

Juvenile Chinook for these tests were raised in our Battelle-Northwest hatchery from eggs secured from Priest Rapids Dam, 43 km upstream. The fish averaged 64.3 mm (standard deviation, 9.9) in length from snout to the hypural plate and 3.8 g (standard deviation, 1.9) in weight when tests were run in July and August. All were acclimated to 15° C. Juvenile rainbow were raised in our hatchery from adult rainbow brood stock maintained for several years. Juvenile rainbows averaged 75.4 mm (s.d., 9.6) in length and 8.0 (s.d., 2.7) grams. Rainbow were not acclimated to a constant temperature, but were held in hatchery water pumped directly from the Columbia River. Temperatures, which were recorded continuously, ranged from about 17 to about 19° C during the tests.

Predators for preliminary Chinook and all rainbow tests were adult rainbow trout more than three-years-old from the hatchery brood stock. Two-year-old rainbows, which were more agile than older adults, were used as predators for the 1969 Chinook tests. Because the northern squawfish, Ptychocheilus oregonensis (Richardson), is an important predator of juvenile salmonids in the Columbia River system (Thompson, 1959), it was initially considered for these experiments. Feeding performance of squawfish in laboratory tanks proved unreliable, however, necessitating selection of an alternate.

Each test was executed according to the flow diagram in Figure 1 -- (See Appendix A). Juvenile fish were first removed from a common stock tank and both test and control groups were marked by a liquid nitrogen cold brand (Fujihara and Nakatani, 1967). After a minimum of 72 hours for recovery from handling and for appearance of a strong brand, each group was transferred to a different tank, one containing heated water, the other

containing water at acclimation temperature. Thermal exposure tanks were supplied with flowing water that had been air-equilibrated after heating to avoid additional stress from gas supersaturation. Temperatures were maintained by a control valve (Model PX9700, Automatic Controls Co.) that mixed hot and cold water supplies.

The shock temperatures selected were 28.0 ± 0.05 °C for Chinook and 30.5 ± 0.05 °C for rainbow. These temperatures are within the lethal ranges for the test species, with median death-times approximately 22-1/2 min and 15-1/2 min, respectively (Coutant and Dean, Nov., 1972). Because of recognized changes (i.e., loss of equilibrium) at a well-defined time prior to death, different times of exposure were administered that were fractions of this median equilibrium-loss dose (ELD). The relationship between equilibrium loss and death in Chinook and rainbow will be discussed in another paper. The median equilibrium loss dose used as a baseline was redetermined at several intervals throughout the rainbow test series to check for possible changes in acclimation. Adjustments were found unnecessary. Figure 2 presents the relationship between doses used in this study and units of time, percent of median death time, and percent of the median equilibrium loss dose.

Upon completion of the timed dose, shocked and control groups were reunited in the acclimation temperature. In tests with no recovery period, the mixed groups were offered within one minute to the predators. Holding periods of one-half or one hour, to test for possible recovery from heat effects, were spent by the mixed groups at acclimation temperature where controls were given the sham dose, followed by simultaneous addition of all fish to the predator tank.

Predation tests were conducted in 4- or 6-foot diameter (1.2 or 1.8 m) circular fiberglass tanks with water depths of 65 and 80 cm, respectively. A continuous exchange of water was maintained at about 15 l/min entering at the perimeter surface and leaving via a double standpipe from the center bottom. The tanks were devoid of structures other than the inlet pipes, outflow standpipe and the tank walls, which would provide visual protection

to the fry. Mossman (1955) discusses the theoretical effectiveness of tank walls as cover (by limiting the angles of attack and necessitating "braking" by the predator to avoid collision); practical concerns limited our compensating for such effects. New predators soon learned to avoid long-range lunges for prey and developed a technique of close approach and short jabs.

After introduction of fry, the predators were allowed a maximum of one-half hour to remove approximately 50% of the prey. The survivors were removed, and test and control fish were counted. Rainbow prey were then placed under refrigeration until length and weight determinations were made.

A longer predation period was considered unsuitable due to possible recovery of prey fish from thermal shock effects. Predators required some training to accept living prey readily after years of artificial hatchery feed, but once trained, they generally consumed the required number of fish within 3 to 10 minutes.

The reason for limiting the level of predation is the change in ratio of prey availability during a test, i.e., the decrease in relative abundance of the preferred group throughout the period of exposure to predation (Bams, 1967). The measured predation rate of the preferred group, based on the results of the overall test, is lower than the actual instantaneous rate for that group. This feature increases as predation continues within a test. To keep the variation in availability ratios within reasonable limits and the predation rates thus measured comparable, Bams chose to standardize the overall level of predation. His suggestion was adopted for this study. This procedure was difficult to adhere to in practice, however. Several tests were voided because predation was stopped prematurely or too late. Tests were not considered valid if more than 35 or fewer than 15 fish remained. The results given for a particular test include a bias proportional to the indicated rates of predation and the difference between the total fish remaining and 25. Estimation of this bias is not easily made and it was therefore not carried out.

Surviving fry were not used in subsequent trials as a precaution against learning or long-term effects of thermal shock. Predators were

used repeatedly, however, as often as they were able to consume 25 fish within a half-hour period. There was no indication that predator groups increased their selectivity for a given group of prey after several tests.

The statistic chosen by Bams (1967), and used in this study to express the difference in predation rates upon the two groups of fish is the ratio $d_p = \frac{i_1}{i_2}$, where i_1 and i_2 are, respectively, the instantaneous mortality rates of the first (shocked) and the second (control) group. The determination of i is achieved as follows. If one assume a constant mortality rate of test (or control) fish from one time interval to another within a test, then loss of fish is proportional to population size at termination of the test. If the time of death for each test fish could be recorded, the data could be fit by regression analysis to get $S = Ie^{-i(t)}$, where S = the number of test fish remaining at completion of the test, I = the initial number of fish, i = instantaneous mortality rate, and t = time. But if we are only able to determine the number of fish at the end of a test, and we express population size as a percentage of the initial number of fish, then for the same sequence of fish deaths we would have the equation $s = 1.00 e^{-i(t)}$, where s = survival proportion, $\frac{\text{No. at finish}}{\text{No. at start}}$. When time is set as a unit interval, we get $s = e^{-i}$, or $i = -\log_e s$, as used by Bams. The chi-square analysis was used to test for significance of observed differences in predation rates.

Fish performance varies greatly with size, and size differences must be considered in predation tests. However, obtaining accurate individual length and weight measurements, while retaining fish in good physical condition immediately prior to an experiment, proved mutually exclusive. Consequently, size data were taken only on survivors from individual tests with juvenile rainbow trout and from stock fish at periodic intervals. Size data were not collected on juvenile Chinook. Lengths of survivors in control and shocked groups from each experiment were tested for significant differences with the t-test. In addition, the lengths in surviving groups were compared with a similar number of lengths selected at random from lengths of stock fish.

RESULTS

Juvenile Rainbow Trout Prey

The results of predation experiments carried out in 1968 are presented in Table 1 (See Appendix A). There was no recovery period in one series of tests, while one-half hour recovery was allowed in a second series. Trends in the differences in predation rates (d_p) for different lengths of thermal exposure (both for individual tests and for all tests in a treatment group) are illustrated in Figure 3.

No recovery. Tests for heterogeneity revealed a consistency within each of the treatment groups of this series, which included 15% through 50% of the equilibrium loss dose. Discussion of treatments, therefore, can be based on the χ^2 on totals ("combined") for each length of thermal exposure. There were no significant differences (95% level) between the numbers of test and control fish consumed after the 15% and 20% exposures. Predators did select significantly more test fish (0.05 or 0.01 levels), however, after the 25%, 30%, 40% and 50% exposures, indicating detriment at these thermal doses.

Extrapolation of the trend in d_p ratios for this series (i.e., the calculated measure of difference in the rates of predation between test and control prey) shows an intercept with 1 (no difference) between the 15 and 20% dose levels (Figure 3). The difference increases steeply, although with a somewhat anomalous decrease at 40%. The pattern is relatively unchanged if one considers a linear regression analysis of, alternatively, the unweighted means of individual d_p 's in the treatment groups or the combined d_p 's, both of which are illustrated. Both regressions are significant (0.05 level) with correlations (relation between dose and d_p) of 0.85 and 0.88, respectively.

One-half hour recovery. Tests for heterogeneity indicated that the 60%, 80% and 100% treatments were homogeneous but that the 50% treatment was not. Discussion of the latter exposures must be based on individual tests. Taken individually, each test in this treatment indicated no

significant difference between consumption of heat shocked and control prey. Based upon χ^2 of totals ("combined"), there were significant differences between predation of test fish and controls at doses of 80 and 100% of the equilibrium loss dose, but no significant difference at 60%.

The group d_p ratios, connected by lines in Figure 3 for clarity, exhibit an apparent trend with an intercept with 1 estimated to be near 50%. There were too few treatments in this series and too few tests within each treatment to allow meaningful regression analysis.

Juvenile Chinook Salmon Prey

Preliminary tests were run in 1968 at exposure levels of 50 and 100% ELD, with no recovery time allowed. The results, which should be considered exploratory, are presented in Table 2.

Tests in 1969 are presented in Table 3. No recovery was allowed in the first series; there was one-half hour recovery in a second series and one set of tests was conducted at 80% ELD with one hour of recovery. Trends in d_p ratios for the "no recovery" and "one-half hour recovery" series are shown in Figure 4A and 4B, respectively.

Preliminary tests, no recovery. Data from four tests on fish exposed to 50% ELD were not consistent. Increased predation on the thermally shocked fish was indicated in all but one test in which an insufficient number of fish (14) was consumed to render a valid representation. Results from the three tests at 100% were homogeneous, and the series demonstrated different predation rates between experimental and control fish.

No recovery. Analysis for heterogeneity indicated that tests within each exposure level of this series (5, 10, 20, 30, and 50%) were consistent, and that discussion can be based upon the combined χ^2 for each exposure. There were significant differences (0.05 level of probability of error) between test and control fish consumed at all doses except 5%.

A clear trend in d_p ratios for this series is evident from Figure 4A. An intercept with 1 (no difference) was suggested near 5 to 10%, with a

rapid rise with increasing thermal dose. Linear regression of d_p ratios for combined tests had a high correlation (0.96), but an exponential model may be more appropriate (dashed line). For comparable exposure times, d_p ratios for Chinook prey exceeded those for rainbow trout prey.

One-half hour recovery. All thermal exposure treatments in this series (20, 40, 50 and 80% of the median equilibrium loss dose) were homogeneous. Only the 80% exposure group yielded a χ^2 on totals that were significant. Examination of d_p ratios (Figure 4B) reveals a slowly rising trend (in contrast to the steep rise without recovery) with increasing thermal doses. An intercept with 1 is suggested at doses near 20%, although variations from 1 at 40% and 50% are so slight as to be insignificant with the number of tests conducted.

One hour recovery. The results of the four tests were homogeneous, and the χ^2 on totals was significant. Despite one-hour recovery time, the surviving fish exposed to 80% of their median equilibrium loss time were eaten at a rate significantly greater than the exposed control fish.

Predation and Fish Length

Surviving shocked and control prey were never significantly different in length. Both were different from stock fish in some tests, however. Of 15 tests for which length data were analyzed in detail, five had survivors with significantly different lengths than the stock. The direction of difference was not consistent, for the survivors were larger in three experiments but smaller in the other two.

DISCUSSION

The tests simulated, in simplified manner, the situation believed extant near the Hanford thermal discharges where the principal thermal shocks are received only by the prey. Here, juvenile salmonids pass with strong river currents through the zone of maximum temperatures (that may exceed 48 °C) while predators wait outside this zone in slightly elevated temperatures (2 to 3 °C) to which they are capable of acclimating metabolically. The principal simplification was exposing the fish to a constant, rather than fluctuating, shock temperatures as occurs in nature (Jaske, Templeton and Coutant, 1970).

Experimental fish were actually subjected to two thermal shocks during the timed thermal dose. The first was an abrupt rise in temperature at the time of transfer to the heated water. The second was an abrupt decrease of similar amount on return to the acclimation temperature. The latter shock induced momentary loss of equilibrium in some fish not showing these symptoms in the heated bath. The independent effects of these two shocks could not be assessed in the experiments, although it is appreciated that "cold shock" may also be important since it occurred just prior to capture by predators.

The effects of thermal shock, without recovery, on predation of these fish were strongly correlated with the duration of exposure to the potentially lethal temperatures, i.e., the thermal dose. It is not clear, however, from the number of tests conducted just what form this relationship generally takes, or whether the dose-response relationship would also be expressed at different temperatures. However, a dose-response relationship, so often seen in studies of direct mortality, also appears to be a suitable model for this secondarily lethal effect of high temperature.

Under controlled conditions of the experiments, differential predation remains a function of a number of factors, some of which were identified by Bams (1967). These factors include discovery rate, attack rate, capture rate, retention, availability, level of predation and relative sizes of predators and prey.

Discovery

A difference in discovery rates by predators between two groups of otherwise simultaneously available fry would constitute a basis for differential predation. Test containers selected for this study offered few physical barriers to the discovery of fry by predators such as might occur in nature. But, as Mossman (1955) discussed, outlet structures, water surface, and tank walls do provide some cover, at least theoretically. When a prey fish approaches the surface, it limits the directions from which discovery (and attack) can come. Attempts were made to ensure that fish from both sources in an experiment mingled freely in the transfer container (a 9-liter plastic pail) and that they were equally exposed to the predators when dumped quickly into the test tank.

Of probable high significance to discovery is the behavior of shocked fish. At the level of thermal dose sufficient to induce median loss of equilibrium, half of the shocked fish have been rendered unable to swim. Most of these fish regain equilibrium on return to cooler water, but their behavior remains abnormal, even to the investigator. Previous studies (Coutant and Dean, Nov., 1972; Tsukuda and Ohsawa, 1958) demonstrated a progression of behavioral changes in water of lethal temperature leading to the well-defined point of equilibrium loss. Such changes involve frequency of bursts of swimming activity, position of fish in the water (e.g., head at the surface, body angled down), and timing and coordination of fin beating, among others. Such patterns likely prompt rapid discovery by a lurking predator. Obviously disoriented prey were, in fact, observed to be eaten quickly in these tests. There was also an observed tendency for prey fish to school, perhaps out of fear of predation. No separate records of differential discovery rate during predation could be made in these experiments, since most individual prey fish could not be identified reliably in the flurry of predatory and escape activity.

Parker, Black and Larkin (1963) suggest that differential recognition requires that the "abnormal" fish be in the minority among the population being tested, and that its abnormality stands out for the predator as a result of the statistical imbalance. Their experiments were designed on

this assumption. Bams (1967), however, used groups of fish supplied in equal numbers and still found consistent predator preference for one group, as in the present study. Other factors may, therefore, be operative at the discovery stage, such as instinctive or learned ability by the predator to quickly perceive particular visual patterns (e.g., the flashing side of a distressed fish). Whereas Bams considered such knowledge by the predator to be remote when comparing hatchery and wild fish having but minute differences, it is a highly plausible factor when the prey fish is injured with a thermal shock and may exhibit observable difference in behavior.

Attack

After discovery of the prey, the predator may attack test and control groups at different rates, i.e. exert selection by accepting or rejecting each potential prey on the basis of a characteristic or group of characteristics that it perceives. McPhail (1969) observed such discrimination in the attack of two races of threespined stickleback (Gasterosteus aculeatus) by the western mudminnow (Novumbra hubbsi) in laboratory tests where predatory activity was slow and easily observed. Fish location may also affect the routes available for the predator to attack. Attack rate is likely important in these experiments.

Abnormal prey behavior patterns described above, which may vary in degree from high to low levels of thermal dose, can provide more suitable cues for initiating pursuit than would the behavior of unshocked fish. Mossman (1955) cites evidence that suggest provocation of attacks by sign stimuli associated with weakness of the prey species. In addition to aberrant swimming behavior, a behavioral change evident in fish subjected to extreme shock was slowness in seeking shelter, however futile this attempt. As with the discovery rate, the basic attack rate parameter could not be established directly in the tests and for the same reasons. Bams (personal communication) suggested, however, that aberrant swimming behavior (flashing, deviations from horizontal position, etc.) may be especially important for predation in nature through enhanced discovery, while attack rate may be more strongly effective in the laboratory where the predator can see many prey simultaneously and choose.

Capture

Once attack is initiated, a difference may occur in the rates of capture between the two groups. Capture is principally dependent upon escape performance of the prey fish. Also, the confines of the test tank may influence capture ratios if the two prey groups do not mix thoroughly. Escape performance is a complex interaction of several prey abilities, including detection of pursuit, burst swimming capacity, agility in changing swimming direction, and capability for a prolonged series of extreme exertions. None of these could be measured independently in these tests. Thus, as with discovery and attack, the statistic for vulnerability to capture must also derive from the overall predation rate. It seems reasonable, however, to ascribe some of the observed differences in predation rates to a differential capture rate. Fish that have undergone long sublethal thermal doses are obviously less responsive to stimulation with a forceps than are unshocked fish from the same source. This change in responsiveness may be manifested in recognition of predators as well, and may be a function of thermal dose. Herting and Witt (1967) ascribed an observed increase in bowfin (Amia calva) predation on starved, diseased or otherwise weakened bluegills (Lepomis macrochirus) and largemouth bass (Micropterus salmoides) to sluggishness in swimming of the weakened prey, although they did not critically test this suggestion.

Retention

A parameter not mentioned by Bams, yet evident in these experiments (particularly when squawfish were tried as predators) is prey retention. Some prey fish were apparently caught (i.e., they show teeth marks) yet were not retained. Bams (personal communication) relates that R. R. Parker (Pacific Biological Station, Fisheries Research Board of Canada) has observed the same phenomenon in coho predation on pink salmon in estuaries. In subsequent, carefully controlled tests, Parker showed that these marked prey were measurably avoided by experienced predators. The possibility of retention differences was not recognized sufficiently early in the experiments for correlation with prey source. Unless obviously regurgitated, the rejected fish were considered alive.

Other Factors

The questions of availability and level of predation were discussed under Materials and Methods. Equal numbers of fish from shocked and control sources were introduced initially to all test tanks, and the experiment was terminated as nearly as possible when half of the fish had been removed.

Experiments by Bams (1967) and others have confirmed the hypothesis that swimming fish performance is strongly correlated with fish length. For proper assessment of differential performance due to factors other than length, the groups compared must be of equal size range. The three sets of measurements made (samples of stock, surviving shocked fish, and surviving control fish) provided some assurance of comparability, since surviving shocked and control fish did not differ significantly in length. Both surviving groups differed from the stock in some tests, suggesting that inadvertent selection for length occurred, either by predators or by the investigator in choosing fish from the stock, but without regard to fish treatment. This apparent selection was not consistent throughout the tests, for survivors were smaller than the stock in some tests but larger in others. The role of length, therefore, appeared to be minor.

Reversibility of Effects

Whatever the causes for differences in predation rates shown by these experiments, they were clearly reversible to some degree with time. When one-half hour was allotted for recovery prior to introduction of mixed prey, plus any additional recovery time during the predation period, the thermal dose required to invoke statistically significant differences in predation rates rose approximately three to four times, from about 20% of the equilibrium loss dose without recovery to about 80%.

The significance of the results appears to extend beyond confirmation of recovery, however, Figures 3 and 4 manifest recovery in two ways that suggest two recovery mechanisms and/or two types of thermal damage. First, as also indicated by statistical tests of significance, there is a shift to the right (toward higher doses) of the point where the d_p ratio equals one. Very short durations of thermal exposure sufficient to increase predation

immediately after the shock no longer induced differences in predation following recovery. The component(s) of performance affected by these short shocks must, therefore, return quickly to normal. Second, there is a decrease in slope of the trend in d_p ratios following a half-hour recovery. This is shown by the Chinook data but less convincingly by the rainbow. The decrease in slope suggests that longer thermal exposures induce a damage for which there is a slow component of recovery. This component may, in fact, never affect complete recovery, a speculation prompted by the single set of tests at 80% ELD in which there remained a significant difference in predation after one hour. Further tests after various recovery times will be required before the recovery sequence is clear.

CONCLUSIONS

These experiments have dealt solely with subjecting juvenile salmonids to differing sublethal thermal doses at arbitrarily-selected lethal temperatures. Further study is desirable at a range of lethal and sublethal shock temperatures in order to determine if there is a consistent relationship between thermal dose causing significantly increased vulnerability to predation and percentage of the equilibrium loss or death doses.

Short, sublethal exposures to potentially lethal high temperatures are capable of incapacitating juvenile salmonids to an extent that the fish are, at least temporarily, more vulnerable to predation. The differences in predation rates provide a quantitative measure of harmful effect and thus the data can be used in scientific design of safe mixing zones for thermal releases to aquatic environments.

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APPENDIX A
TABLES AND FIGURES

TABLE 1. Results of Predation on Juvenile Rainbow Trout by Adult Rainbow Trout. (Acclimation Temperature, 17-19 °C; Shock Temperature, 30.5 °C. Number of fish in each group at start of predation was 25, unless noted.
 $[i = -\log_e (\text{survival proportion}); d_p = \frac{i \text{ shocked}}{i \text{ control}}]$)

Percent		Number Surviving		Chi Square	i		
Equilibrium		Shocked	Control	(1 d.f.)	Shocked	Control	d_p
Loss	Dose						
No Recovery							
	15	9	11	0.200	1.021	0.820	1.244
	15	16	9	1.960	0.446	1.021	0.436
	15	23	16	1.256	0.083	0.446	0.186
Combined		48	36	0.857	0.446	0.734	0.608
Heterogeneity	χ^2			1.559			

	20	22	15	1.324	0.127	0.510	0.250
	20	20	22	0.095	0.223	0.127	1.745
	20	14	20	1.058	0.579	0.223	2.598
	20	14	17	0.290	0.579	0.385	1.503
	20	13	14	0.037	0.653	0.579	1.127
	20	14	9	1.086	0.579	1.021	0.567
	20	10	13	0.391	0.916	0.653	1.401
	20	9	13	0.727	1.021	0.653	1.562

TABLE 1. (contd)

Equilibrium Loss Dose	Number Surviving		Chi Square (1 d.f.)	i		$\frac{d}{p}$
	Shocked	Control		Shocked	Control	
Combined	116	123	0.205	0.544	0.486	1.120
Heterogeneity χ^2			4.793			
25	9	13	0.727	1.021	0.653	1.562
25	6	14	3.200	1.427	0.579	2.461
Combined	15	27	1.714	1.204	0.616	1.954
Heterogeneity χ^2			2.213			
30	11	17	1.285	0.820	0.385	2.128
30	14	23	2.189	0.579	0.083	6.953
30	10	20	3.333	0.916	0.223	4.106
Combined	35	60	6.579	0.761	0.223	3.412
Heterogeneity χ^2			0.228			
40	13	18	0.806	0.653	0.328	1.990
40	8	18	3.846	1.139	0.328	3.468
40	19	21	0.100	0.274	0.174	1.574
40	11	18	1.689	0.820	0.328	2.499
Combined	51	75	4.571	0.673	0.287	2.340
Heterogeneity χ^2			1.870			
50	8	20	5.142	1.139	0.223	5.106
50	5	18	7.347	1.609	0.328	4.899
50	1	20	17.190	3.218	0.223	14.425
50	1	19	16.200	3.218	0.274	11.729
50	2	12	7.142	2.525	0.733	3.441

TABLE 1. (contd)

Equilibrium Loss Dose	Number Surviving		Chi Square (1 d.f.)	i		$\frac{d}{p}$
	Shocked	Control		Shocked	Control	
Combined	17	89	48.905	1.995	0.339	5.873
Heterogeneity χ^2			5.076			

Half-Hour Recovery

50	16	23	1.256	0.446	0.083	5.352
50	9 ¹	3	3.251	0.980	2.120	0.462
50	7 ¹	16	3.165	1.232	0.446	2.760
50	16 ¹	10	1.641	0.405	0.916	0.442
Combined	48	52	0.0613	0.703	0.653	1.075
Heterogeneity χ^2			9.25			
60	11 ⁴	23	2.423	0.646	0.083	7.755
60	17 ²	17	0.059	0.302	0.385	0.783
Combined	28	40	0.866	0.451	0.223	2.025
Heterogeneity χ^2			1.61			
80	4 ¹	21	10.881	1.791	0.174	10.276
80	13	16	0.310	0.653	0.446	1.465
80	11	24 ⁵	4.828	0.820	0.040	20.111
80	14	18	0.500	0.579	0.328	1.765
Combined	42	80	11.457	0.857	0.223	3.842
Heterogeneity χ^2			5.67			
100	12 ³	20	1.113	0.606	0.223	2.716
100	6 ³	17	3.966	1.299	0.385	3.368
100	15 ¹	19	0.321	0.470	0.274	1.712
Combined	33	56	3.914	0.723	0.292	2.474
Heterogeneity χ^2			1.49			

TABLE 1. (contd)

¹	24 fish at start of predation
²	23 fish at start of predation
³	22 fish at start of predation
⁴	21 fish at start of predation
⁵	No fish eaten, but one assumed eaten for purposes of calculation

TABLE 2. Results of Predation on Juvenile Chinook Salmon by Adult Rainbow Trout. (Acclimation Temperature, 15 °C; Shock Temperature, 28 °C. Number of fish in each group at start of predation was 25. No recovery. Column headings are explained in Table 1.)

Percent						
Equilibrium	Number Surviving		Chi Square	i		
Loss Dose	Shocked	Control	(1 d.f.)	Shocked	Control	d _p
50	5	17	6.545	1.609	0.385	4.173
50	15	21	1.000	0.510	0.174	2.929
50	1	24 ¹	21.160	3.218	0.040	78.851
50	3	13	6.250	2.120	0.653	3.242
Combined	24	76	27.040	1.427	0.274	5.200
Heterogeneity χ^2			8.908			
100	5	16	5.761	1.609	0.446	3.450
100	1	21	18.181	3.218	0.174	18.461
100	2	23	17.640	2.525	0.083	30.291
Combined	8	60	39.764	2.238	0.223	10.029
Heterogeneity χ^2			1.819			

¹No fish eaten, but one assumed eaten for purposes of calculation

TABLE 3. Results of Predation on Juvenile Chinook Salmon by 2-Year-Old Rainbow Trout. (Acclimation Temperature, 15 °C; Shock Temperature, 28 °C. Number of fish in each group at start of predation was 25, unless noted. Column headings are explained in Table 1.)

Percent						
Equilibrium	Number Surviving		Chi Square	i		
Loss Dose	Shocked	Control	(1 d.f.)	Shocked	Control	d _p
No Recovery						
5	8	10	0.222	1.139	0.916	1.243
5	9	13	0.727	1.021	0.653	1.562
5	11	14	0.360	0.820	0.579	1.415
5	9	14	1.086	1.021	0.579	1.762
5	13	13	0	0.653	0.653	1.000
5	8	8	0	1.139	1.139	1.000
5	15	12	0.333	0.510	0.733	0.695
Combined	73	84	0.770	0.874	0.733	1.191
Heterogeneity χ^2			1.96			
10	3	22	14.440	2.120	0.127	16.586
10	10	19	2.793	0.916	0.274	3.338
10	13	16	0.310	0.653	0.446	1.465
10	14	22	1.777	0.579	0.127	4.535
10	9	22	5.451	1.021	0.127	7.992
10	8	13	1.190	1.139	0.653	1.742

TABLE 3. (contd)

Percent						
Equilibrium	<u>Number Surviving</u>		Chi Square	<u>i</u>		
<u>Loss Dose</u>	<u>Shocked</u>	<u>Control</u>	<u>(1 d.f.)</u>	<u>Shocked</u>	<u>Control</u>	<u>d_p</u>
Combined	57	114	19.000	0.967	0.274	3.525
Heterogeneity χ^2			6.96			
20	6	18	6.000	1.427	0.328	4.344
20	3	24	16.333	2.120	0.040	51.939
20	8	21	5.827	1.139	0.174	6.535
20	7	23	8.533	1.272	0.083	15.266
Combined	24	86	34.945	1.427	0.150	9.462
Heterogeneity χ^2			1.75			
30	3	23	15.384	2.120	0.083	25.428
30	1	22	19.173	3.218	0.127	25.180
30	2	22	16.666	2.525	0.127	19.757
30	1	23	20.166	3.218	0.083	38.604
Combined	7	90	71.020	2.659	0.105	25.239
Heterogeneity χ^2			0.37			
50	1	24	21.160	3.218	0.040	78.851
50	1	24	21.160	3.218	0.040	78.851
Combined	2	48	42.320	3.218	0.040	78.851
Heterogeneity χ^2			0.000			

TABLE 3. (contd)

Percent						
Equilibrium	Number Surviving		Chi Square	i		
<u>Loss Dose</u>	<u>Shocked</u>	<u>Control</u>	<u>(1 d.f.)</u>	<u>Shocked</u>	<u>Control</u>	<u>d_p</u>
Half-Hour Recovery						
20	11	14	0.360	0.820	0.579	1.415
20	10	14	0.666	0.916	0.579	1.580
20	15	14	0.034	0.510	0.579	0.881
20	12	16	0.571	0.733	0.446	1.644
20	11	11	0	0.820	0.820	1.000
20	12	12	0	0.733	0.733	1.000
Combined	71	81	0.657	0.747	0.616	1.213
Heterogeneity χ^2			0.97			

40	5	10	1.666	1.609	0.916	1.756
40	10	14	0.666	0.916	0.579	1.580
40	10	14	0.666	0.916	0.579	1.580
40	9 ¹	14	0.892	0.980	0.579	1.691
Combined	34	52	3.588	1.068	0.653	1.634
Heterogeneity χ^2			0.30			

50	12 ¹	20	1.687	0.693	0.223	3.106
50	12	11	0.043	0.733	0.820	0.894
50	8 ²	16	2.045	1.056	0.446	2.366
50	9 ¹	11	0.126	0.980	0.820	1.194
Combined	41	58	2.267	0.850	0.544	1.561
Heterogeneity χ^2			1.63			

TABLE 3. (contd)

Percent		Number Surviving		Chi Square (1 d.f.)	i		d_p
Equilibrium	Loss Dose	Shocked	Control		Shocked	Control	
	80	9	17	2.461	1.021	0.385	2.649
	80	5	21	9.846	1.609	0.174	9.230
	80	9 ²	20	3.311	0.938	0.223	4.204
	80	8 ¹	12	0.645	1.098	0.733	1.496
Combined		31	70	13.898	1.140	0.356	3.198
Heterogeneity χ^2				2.36			
One Hour Recovery							
	80	9 ²	16	1.422	0.938	0.446	2.102
	80	12 ³	14	0.004	0.606	0.579	1.045
	80	3 ²	16	7.858	2.036	0.446	4.564
	80	7 ⁴	15	0.911	0.944	0.510	1.848
Combined		31	61	5.820	1.020	0.494	2.064
Heterogeneity χ^2				4.38			

¹24 fish at start of predation²23 fish at start of predation³22 fish at start of predation⁴18 fish at start of predation

FIGURE 1. Flow Diagram for Differential Predation Tests

FIGURE 2. Relationships Between Thermal Dose Used in the Text (Percent of the Median Equilibrium Loss Dose) and (1) Median Time to Equilibrium Loss (EL), (2) Median Time to Death (D), and (3) Percent of Median Death Dose. (Derived from unpublished data, C. C. Coutant and J. M. Dean).

FIGURE 3. Pattern of d_p Ratios with Increasing Thermal Doses, Juvenile Rainbow Trout with (A) No Recovery, and (B) One-Half Hour Recovery.

FIGURE 4. Pattern of d_p Ratios with Increasing Thermal Doses, Juvenile Chinook Salmon with (A) No Recovery, and (B) One-Half Hour Recovery. Scale of A is twice that of B and Figure 3.

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